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Decomposition as a regulator of carbon accretion in mangroves: a review

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ABSTRACT

The production and decomposition of litter in mangroves plays a significant role in the nutrient and organic carbon cycles. These can be highly variable both spatially and temporally as a result of numerous factors including tidal range, forest type, abundance and type of herbivorous fauna, temperature, and microbial activity. Mangroves also play an important role in blue carbon sequestration, with their status as carbon sinks crucial in mitigating against greenhouse gas-induced climate change. Blue carbon is a term used to describe the carbon captured by oceans and coastal ecosystems. We review and discuss the current available knowledge regarding sources of organic matter (OM) in mangroves as well as the roles of benthic macrofauna, water and microbial activity in the decomposition of OM in order to gain a better understanding of the decompositional processes that take place. Macrofauna break down and bury litter, thereby improving litter quality, in turn increasing decomposition rates via leaching and microbial activity. Microbial decomposition in mangroves is slow as a result of phenolic concentrations in the litter. A build-up of phenolic compounds inhibits microbial activity leading to the accumulation of OM in mangroves. Although knowledge has improved, there are still gaps in the information available and we still have an incomplete picture of the decompositional process in mangroves, and in particular the formation of blue carbon stores, necessitating further research.

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1. Introduction

Mangrove forests are highly productive ecosystems that occur in the intertidal zones of the tropics and sub-tropics (Bouillon et al., 2008a; Keuskamp et al., 2015; Mitsch and Gosselink, 2015). These intertidal forests play an important role in coastal ocean biogeochemistry as they act as nutrient filters between land and sea (Sanders et al., 2010a; Bouillon et al., 2008a; Castillo et al., 2017). Their nutrient cycles are closely linked with those found in the adjacent water (Alongi, 1996). Mangroves also play a significant role in the total organic carbon (TOC) oceanic cycle (Sanders et al., 2010b) as they have the capacity to efficiently trap, uptake and recycle suspended litter in the water column (Twilley et al., 1986; Kristensen et al., 1994; Middleburg et al., 1996; Sanders et al., 2012).

Decomposition is an important process that controls the flux of carbon and nutrients in mangroves (McKee and Faulkner, 2000). Due to the imbalance between rates of organic matter (OM) production and decomposition, mangroves and other vegetated coastal ecosystems represent an important global carbon sink (Donato et al., 2011; Yuan et al., 2015). As such, mangroves are receiving growing attention in the climate change debate in relation to their capacity for so-called "blue carbon" sequestration. In this context, the estimated 30–50% reduction in mangrove coverage reported in recent decades (Donato et al., 2011) is a significant concern.

The magnitude and fate of OM in mangroves is highly variable both temporally and spatially because they are regulated by numerous factors such as soil type and texture, tidal rage and elevation, bioturbation intensity, forest type, abundance of herbivorous fauna, redox state, temperature and rainfall (Middelburg et al., 1996; Ashton et al., 1999; Sukardjo and Alongi, 2013).

In this report, we review and evaluate the current knowledge regarding the decomposition of OM in mangrove ecosystems. We will discuss the various sources of OM and review the different decomposition processes that take place in mangroves, including leaching, litter grazing by macroinvertebrates and microbial decomposition, with an emphasis on carbon, nitrogen and phosphorous cycles. Developing a more comprehensive understanding of decomposition processes in these systems is vital given their important role in sequestering blue carbon, and potentially mitigating against climate change.

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2. Sources of organic matter in mangroves

There are a range of sources that contribute to the OM found in mangroves. The two primary sources are litter fall from trees, which is composed primarily of leaves, propagules, fallen tree stems and branches along with subsurface roots (Tam and Wong, 1998; Bouillon et al., 2004; Kristensen et al., 2008). Organic matter inputs also consist of production by micro- or macro-algae, phytoplankton production in the local water column (autochthonous inputs) and marine or riverine material such as seagrasses (allochthonous inputs) (Bouillon et al., 2004; Kristensen et al., 2008).

2.1. Primary productivity

The primary means of estimating the input rate of OM in mangroves is using primary production (Kristensen et al., 2008). Litter production is one of the three main components of net forest primary productivity and therefore a useful indicator of primary productivity (Mfilinge et al., 2005; Sukardjo and Alongi, 2013). It is estimated that litter fall from mangroves equates to approximately 30%–60% of net primary production in forest ecosystems (Ashton et al., 1999; Alongi et al., 2005; Malhi et al., 2011; Alongi, 2014); with global average litter fall rates of 38 mol C m^{-2} yr^{-1} (Kristensen et al., 2008). However, production rates can vary widely throughout the globe with the highest rates observed in tropical regions (lowest latitudes), and rates decreasing linearly with increasing latitude (sub-tropical regions; Twilley et al., 1992). Litter production also varies between species (Hossain and Hoque, 2008) along with percentage contribution between leaves, fruits, flowers, stipules and twigs which can also vary seasonally (Mfilinge et al., 2005; Hossain and Hoque, 2008; Kamruzzaman et al., 2017).

Litter production can also be dependent upon flood duration. A study conducted by Krauss et al. (2006) identified that *L. racemose* distributed more biomass to leaves and stems than to roots with greater flood duration, as opposed to *A. germinans*, which distributed more biomass to its roots. *R. mangle* appeared to be unaffected by flood duration.

Relying solely on litter fall may give a skewed estimate of primary production as mangroves can also be efficient at trapping suspended material from the water column, trapping on average 30% of sediment (Victor et al., 2004) with records as high as 80% (Furukawa et al., 1997). Other sources of primary productivity in mangroves are known to vary substantially; microphytobenthos, phytoplankton and benthic macroalgae rates of productivity are reported to range between 7 and 73 mol C m^{-2} $year^{-1}$, 0.7–21 mol C m^{-2} $year^{-1}$, and 110–118 mol C m^{-2} $year^{-1}$ respectively (Kristensen et al., 2008). Ray and Shahraki (2016), in their survey of an Indian and Iranian mangrove system also showed that the contribution from different carbon sources may show significant seasonal variation.

3. The role of benthic macrofauna in organic matter decomposition

Mangrove forests are an important habitat for a diverse community of benthic fauna which are typically dominated by burrowing decapods such as grapsid crabs, fiddler crabs and sesarmine crabs (Kristensen et al., 2008; Kristensen, 2008; Bouillon et al., 2008b; Mfilinge and Tsuchiya, 2008). The macrofauna are important biotic agents in the regulation of mangrove productivity (Lee, 1999). The foraging and feeding activity of the macrofauna are reported to influence the rate of OM export, decomposition, and nutrient cycling (Lee, 1999; McKee and Faulkner, 2000; Middleton and McKee, 2001; Bosire et al., 2005; Mfilinge and Tsuchiya, 2008; Bouillon et al., 2008b; Kristensen and Alongi, 2006; Kristensen et al., 2008; Kristensen, 2008).

Due to their dominance, a large majority of studies conducted on macrofauna in mangroves have focused on crabs and in particular, sesarmid and fiddler crabs. Crabs have been identified as ecosystem engineers due to the fact that the construction of their burrows modify physical structures, substance chemistry and transport conditions which alter the availability of resources for microbial, faunal and plant communities (Schories et al., 2003; Kristensen, 2008).

3.1. Macrofauna feeding activities

Although previously believed to be of negligible influence, macrofauna substantially reduce litter export through litter consumption (Lee, 1999; Kristensen et al., 2008; Mfilinge and Tsuchiya, 2008). A study conducted by Robertson (1986) identified that sesarmine crabs could remove at least 28% of litter produced in mixed *Rhizophora* forests through consumption and burial in their burrows. Invertebrates have been found to triple surface litter decomposition rates in intertidal areas (Middleton and McKee, 2001). This influence is likely due to the fact that the majority of their diet is composed of leaf litter. Malley (1978) identified that the stomach contents of the sesarmine crab was more than 95% by volume mangrove leaf fragments.

Camilleri (1992) identified macrofauna as a primary link in the mangrove forest food web. Their study determined that feeding on detritus directly influences the rate of decomposition and that macrofauna have the ability to increase the rate of leaf litter turnover by as much as 75 times, than if they weren't present. Additionally, through analyzing the stomach and rectum contents of *Sesarma erythrodactyla* crabs Camilleri (1992) identified that crabs have a preference for partially aged *Rhizophoa stylosa* and *Ruguiera gymnorrihza* litter. Mfilinge and Tsuchiya (2008) later built on these findings and identified a preference for aged or slightly senescent litter which is believed to be a result of lower C/N ratio and higher nutritional value in aged leaves or lower tannin content as it is known to be aversive to detritivores (Bosier et al., 2005).

Crab feeding activities have also been found to affect the quality of litter. When litter is consumed by macrofauna, the plant tissues are broken down, simplifying the structure and the chemical composition and in turn freeing plant cell contents cellulose and hemicellulose from degradation-resistant materials such as lignin (Camilleri, 1992) which facilitates degradation by microorganisms (Camilleri, 1992; Lee, 1999; ; Bosier et al., 2005). Macrofauna and in particular sesarmine crabs also ensure a continuous supply of particulate organic matter (POM) through the production of fecal material which is further decomposed by microorganisms or exported from the mangrove environment (Camilleri, 1992; Lee, 1999).

3.2. Macrofauna foraging activities

Crab foraging activities also influence decomposition. Middleton and McKee (2001) identified that crabs plaster leaves on the walls of their burrows and in doing so increase the rate of decomposition by 2.4 times when compared to litter on the soil surface. This increase in decomposition is likely due to the increase in pore water exchange and sediment chemistry (Lee, 1999).

Additionally, bioturbation affects sediment topography and biogeochemistry through the modification of particle size distribution, redox conditions, drainage and OM and nutrient content (Kristensen, 2008). Crab burrows can affect ground water flow and sediment chemistry, all of which influence the decomposition of OM (Lee, 1999). The effect is likely to vary depending on the species since each species has different burrowing techniques resulting

in different burrow configurations and dimensions (Kristensen, 2008).

Crabs are capable of removing 30–90% of litter fall, thereby substantially reducing the quantity of litter that is exported (Robertson, 1986; Micheli, 1993; Slim et al., 1997; Schories et al., 2003; Kristensen et al., 2008). Bachok et al. (2003) found that mangrove detritus also plays a significant role in the diet of the mud clam (*Gelonia coaxans*) suggesting a potential underestimation of the role of other macrofauna species in the decomposition of OM by focusing primarily on crabs.

4. The role of water in organic matter decomposition

4.1. Leaching

When litter falls from the mangroves and comes into contact with water, there is a very rapid initial loss of mass due to leaching (Ashton et al., 1999). Differential flooding caused by tidal fluctuations is known to influence the decomposition of OM in mangroves (Steinke et al., 1983; Benner et al., 1990; France et al., 1997; Dittmar and Lara, 2001; Romero et al., 2008; Bosire et al., 2005; Kristensen, 2008). Part of the early decomposition of mangrove litter begins with leaching of soluble organic substances (Kristensen, 2008) with the most rapid release of dissolved organic matter (DOM), including organic carbon and nitrogen, and tannins (Ashton et al., 1999) occurring prior to its incorporation into the sedimentary mix (Dittmar and Lara, 2001).

A majority of studies of mangrove litter have focused on leaf litter (Cundell et al., 1979; van der Valk and Attiwill, 1984; Camilleri and Ribi, 1986; Benner et al., 1990; Robertson et al., 1992; Steinke et al., 1993; Ashton et al., 1999). Leaching in leaf litter occurs over a period of 3–28 days (Cundell et al., 1979; Steinke et al., 1993). The rates of mass loss due to leaching range from 14 to 40% (Benner et al., 1990; Ashton et al., 1999; van der Valk and Attiwill, 1984; Camilleri and Ribi, 1986) with rates of organic carbon loss between 20–40% in newly fallen leaf litter (Kristensen, 2008).

It is likely however, that the percentage mass of OM lost due to leaching is over-estimated as it does not include the other components that make up the biomass of OM in mangroves such as woody material. McKee and Faulkner (2000) showed that the percentage of leaves in litter can vary between 46 and 81% indicating that the other components can account for as much as 54% of litter. Additionally, by focusing primarily on leaves, the effect of leaching on the subsurface roots that also contributes mangrove OM (McKee and Faulkner 2000; Kristensen et al., 2008) is not well accounted for. Romero et al. (2005) looking at the loss of mass due to leaching in wood disks reported percentage mass loss similar to the 0.2–27% recorded by France et al. (1997) following a leaching period of 2–7 weeks, which is longer than the recorded leaching periods for the leaves. Additionally, between 17% and 68% of total phosphorous in wood leached out during the first two months of decomposition. The rate of OM loss due to leaching may also be over-estimated due to the fact that many of the studies have been conducted in leaf litter bags. Whilst these successfully exclude macroinvertebrates they cannot exclude microorganisms such as bacteria which are known to play a role in the decomposition of organic matter (Shi et al., 2010; Keuskamp et al., 2015).

Although the phenolic compounds (e.g. tannins) found in mangrove leaf litter may inhibit microbial activity, due to the effect of the 'enzymic latch', (Freeman et al., 2001; Freeman et al., 2004; Saraswati et al., 2016), it is unlikely to inhibit all activity prior to leaching as labile carbon is still available in the fresh litter. This is utilized by microorganisms to produce exoenzymes (Keuskamp et al., 2015). Studies have been conducted comparing percentage mass loss between samples suspended in the air and those influenced by sea water (Ashton et al., 1999), but these do not take into account the fact that the microorganisms that influence decomposition reside in the sediment (Holguin et al., 2001) and the suspended samples are not exposed to the microorganisms.

4.2. Influence of tidal frequency on decomposition

The frequency of flooding due to tidal action can also affect the rate of decomposition. Several studies have identified that decomposition rates are highest in subtidal zones where there is more frequent flooding (Twilley et al., 1986). However, Feller et al. (2002) found lowest rates of decomposition in permanently flooded subtidal zone and upper intertidal zones with decomposition occurring faster in intertidal zones. Middleton and McKee (2001) theorized that tidal flushing creates optimal physico-chemical conditions for decomposition.

5. The role of microbial activity in sedimentary decomposition

Microorganisms play an important role in the degradation of litter through the production of extracellular enzymes that break down complex organic matter into simple compounds such as glucose, amino acids and phosphate (Alongi et al., 1993; Newell, 1996; Holguin et al., 2001; Keuskamp et al., 2015). The degradation of litter fall occurs as soon as it has been colonized by fungi and bacteria that reside in the sediment (Holguin et al., 2001). Microbial decomposition occurs under aerobic and anaerobic conditions via a number of different electron acceptors (Harvey et al., 1986; Newell, 1996; Li et al., 2009). Aerobic decomposition of OM in mangroves occurs on the fresh litter and detritus deposited at or near the sediment surface (Holguin et al., 2001; Kristensen et al., 2008). Anaerobic decomposition occurs in the remainder of the sediment below, as aerobic respiration consumes so much oxygen, little is available to penetrate depths greater than 2 mm below the surface (Holguin et al., 2001; Kristensen, 2008). The exception is the aerobic zone created by roots and the burrows constructed by macroinvertebrates (Kristensen and Alongi, 2006; Kristensen et al., 2008).

Bacteria and fungi constitute 91% of microbial biomass in tropical mangroves, whereas protozoa and algae only make up 2% and 7% respectively (Alongi, 1988; Holguin et al., 2001). In mangrove ecosystems there are five major bacteria types responsible for decomposition, namely, nitrogen fixing, phosphate solubilizing, sulphate reducing, methanogenic, and enzyme producing (Sahoo and Dhal, 2009). There are several other types of bacteria that can be present in mangroves depending upon inputs into the ecosystem, such as iron reducing bacteria that are more common in mangroves located in areas affected by mining (Panchanadikar, 1993). Mangrove ecosystems are also home to manglicolous fungi, a group of fungi that are important for nutrient cycling and are able to synthesize the necessary enzymes required to degrade cellulose, lignin and other plant components (Sahoo and Dhal, 2009).

Microbial decomposition of organic carbon in mangrove sediment is generally slow (Kristensen, 2008). This is due to the high levels of recalcitrant compounds (e.g. tannins, lignin, and cellulose) that are found in mangrove OM (Kristensen, 2008). Although cellulose and lignin can be readily degraded under aerobic conditions, they are degraded slowly under predominantly anaerobic conditions (Hawkins and Freeman, 1994). Dittmar and Lara (2001) found that lignin in mangrove leaf litter (primarily Rhizophora mangle) has a half-life of 150 years in the upper 1.5 m of the sediment (Dittmar and Lara, 2001). This slow degradation is a contributing factor to the accumulation of OM in some mangrove forests (Jennerjahn and Ittekkot, 2002).

Under anaerobic conditions, fermenting prokaryotes first split large molecules into small moieties, after which they are oxidized to CO_2 by a range of anaerobic microorganisms (Kristensen et al., 2008). The anaerobic microorganisms utilize electron acceptors according to energy yield in the following sequence: Mn^{4+}, NO_3^-, Fe^{3+}, and SO_4^{2-} (Kristensen et al., 2008).

Sulphate reduction, both aerobically and anaerobically, is usually considered the most important respiration process in mangrove sediments (Kristensen et al., 2008) accounting for 75–125% of total mineralization (Alongi et al., 1998). Variation in sulfate reduction has been identified as being at least partially the result of stand type and age. Alongi et al. (1998) conducted a study along the northwest coast of peninsular Malaysia and found that sulfate reduction accounted for approximately 75% of carbon oxidation in a 60 year old stand, and could support all of the carbon oxidation (mean = 125%) in a 15 year old stand. Alongi et al. (2000) identified differences between forest type with *Rhizophora* forests having higher rates of sulfate reduction than *Avicennia forests*.

Methane production through fermentative disproportionation of low molecular compounds such as acetate or through the reduction of CO_2, has been found to be relatively low in mangrove ecosystems with emissions ranging from 0 to 5 mmol m^{-2} d^{-1} (Kristensen et al., 2008). However, it is believed that anthropogenic impacts such as increased organic and nutrient loading may increase methane emissions from mangrove sediment through the induction of severe oxygen stress and the supply of labile organic carbon (Kristensen et al., 2008).

Decomposition rates have also been found to be affected by forest type. Alongi et al. (2000) compared *Avicennia* and *Rhizophora* and found that anaerobic respiration was up to three times higher in *Avicennia* forests. Additionally, Ashton et al. (1999) also found that *Sonneratia alba* leaves decompose faster than *Rhizophora apiculata* leaves which has been attributed to *Rhizophora apiculata* containing higher concentrations of recalcitrant compounds and could possibly explain different rates of OM accumulation between different mangroves.

Rates of OM accumulation in mangrove ecosystems are not entirely determined by phenolic compound concentration. Saraswati et al. (2016) conducted a study to assess whether the 'enzymic latch', that is responsible for the accumulation of carbon stores in peatlands (Freeman et al., 2001, 2004) is present in mangrove ecosystems. The 'enzymic latch' is the inhibition of phenol oxidase activity, the enzyme responsible for the decomposition of phenolic compounds, through the build-up of phenolics as a result of anaerobic conditions in the soil (Freeman et al., 2001). Saraswati et al. (2016) identified that the 'enzymic latch' likely causes the accumulation of peat in red mangroves (*Rhizophora mangle*) as identified by the lower hydrolase enzyme activity in anaerobic conditions (phosphatase: −44%; β-glucosidase: −14%; and glucosaminidase: −11%) when compared to aerobic conditions; which could possibly explain the accumulation of peat in all mangroves. However, because red mangroves have been identified as having higher tannin concentrations in their litter (Ashton et al., 1999), it is possible that the 'enzymic latch' may not occur in mangroves with litter containing lower phenolic concentrations. Saraswati et al. (2016) refer to the potential for an ecoengineering approach involving supplementing mangrove systems with phenolic-rich substances to inhibit degradation, following the technique suggested by Freeman et al. (2012) for peatland environments.

6. The role of microbial activity as it relates to nitrogen and phosphorous in mangroves

There are numerous factors that influence nutrient cycles in mangrove ecosystems (Middelburg et al., 1996) and nutrient recycling is an important process in determining whether a mangrove ecosystems is acting as a nutrient source or a nutrient sink (McKee and Faulkner, 2000). Although mangroves are often rich in OM which is an important source of nutrients (McKee and Faulkner, 2000), they have been identified by many as being deficient in nutrients, in particular nitrogen (N) and phosphorous (P) (Sengupta and Chaudhuri, 1991; Alongi et al., 1993; Middelburg et al., 1996; Vazquez et al., 2000; Holguin et al., 2001). That being said, mangrove ecosystems have been identified as having areas of varying nutrient content (Tam and Wong, 1998) with their sediments having been described as being nitrogen rich as compared to their litter (Middelburg et al., 1996). Despite the difference in findings, mangrove ecosystems have been identified as being highly productive and this productivity has been explained by an efficient nutrient recycling system where scarce essential nutrients are retained and new nutrients are made available from litter decomposition (Holguin et al., 2001).

The decomposition of mangrove leaves following their deposition on the soil surface begins with an initial phase in which N and P concentrations decrease followed by a significant increase in N and P in the degrading material (Lin and da Silveria Lobo Sternberg, 2007). Nitrogen fixation, the process involving the conversion of gaseous forms of nitrogen (N_2) into combined forms (i.e. ammonia and organic nitrogen) by bacteria and cyanobacteria (Sahoo and Dhal, 2009), has been reported to account for 13–21% of N immobilization in the microbial community responsible for decomposing *Rhizophora mucronata* leaves (Woitchik et al., 1997). The high rates of nitrogen fixation linked to mangrove ecosystems are associated with the high rates of accumulation of biodegradable OM (up to 4.2 mg N m^{-2} day^{-1}) (Holguin et al., 2001; Sahoo and Dhal, 2009). The litter, pneumatophores, cyanobacterial mats covering the sediment surface and the sediments themselves provide energy for N_2 fixation which has a high energy cost (Holguin et al., 2001; Sahoo and Dhal, 2009). Studies have shown that nitrogen fixation due to the decomposition of leaves, the rhizosphere and superficial sediments in a mangrove ecosystem can account for up to 40%–60% of the annual nitrogen requirement (Zuberer and Silver, 1978; van der Valk and Attiwill, 1984; Holguin et al., 2001), indicating that nitrogen fixation is a major bacterial activity in mangroves, second only to carbon decomposition by sulfate-reducing bacteria (Holguin et al., 2001). Chen and Twilley (1999) found that highest N mineralization rates typically occur to a depth of 0–40 cm with mineralization rates rapidly decreasing with depth.

A study conducted by Toledo et al. (1995) in Mexico looking at N_2 fixation associated with *A. germinans* aerial roots showed that rates were up to 10 times higher during the summer months as compared to autumn and winter months, indicating that temperature plays a large role in N fixation. Bearing this in mind, climate change and the associated temperature fluctuations (Walther et al., 2002) could potentially have implications on N fixation in mangrove ecosystems.

The reduction in P concentrations in detritus is usually assumed to be the result of the precipitation of phosphates due to the abundance of cations in the interstitial water of mangrove sediments which makes phosphates unavailable to plants (Holguin et al., 2001). However, the anaerobic conditions in mangrove sediments would likely favour the dissolution of non-soluble phosphate through the production of sulfide, (Holguin et al., 2001) but this area is largely unstudied (Vasquez et al., 2000).

Vasquez et al. (2000) investigated the phosphate-solubilizing potential of mangrove rhizosphere microbial community when roots of black (*Avicennia germinans*) and white (*Laguncularia racemose*) mangroves from a mangrove ecosystem in Mexico were incubated with culture media supplemented with insoluble, tribasic calcium phosphate. They identified nine strains of phosphate-solubilizing bacteria from the black mangrove roots

and three strains from the white mangrove root. Under lab conditions, *Bacillus amyloliquefacines* (10^8 cfu ml^{-1}), a strain isolated from the black mangrove roots, solubilized an average of 400 mg of phosphate per liter of bacterial suspension which theoretically could supply the daily requirements of a small terrestrial plant (Holguin et al., 2001). These findings indicate that there is a possibility that phosphate-solubilizing bacteria could play a large role in phosphate-solubilization in mangrove ecosystems. However, one clear trend is that phosphorous concentrations decrease with depth (Chen and Twilley, 1999) which could potentially be the result of tannins inhibiting microbial activity (Keuskamp et al., 2015).

7. Conclusion

Understanding decomposition processes in mangroves is critical for assessing the potential for mangroves to act as blue carbon sinks. Although a large number of studies have increased the knowledge base regarding decomposition in mangroves, we still lack a complete understanding of the mechanisms involved both spatially and temporally. Although some trends have been identified, such as the increase in OM content in soil further inland, the roles of vegetation type, tidal function, faunal community structure and microbial processes are still not entirely clear. As many of these factors play an important role in decomposition, it is likely that there will not be a global pattern, but instead more localized patters as they are influenced by local conditions including species of macrofauna, climate, sediment composition and management practices. In order to determine if such pattern exist, we will need to increase the data available in these areas.

One particular area requiring significantly more research is that of how phenolics influence the rate of decomposition in mangroves. An improved understanding of the formation of peat in these coastal zones will provide a better understanding of the carbon budget within mangroves which may unlock further opportunities for carbon sequestration through ecoengineering in the future. Further work may identify methods for maximising the suppression of OM decomposition through the strengthening of the enzymic latch, allowing mangroves to be used as a form of bio-geoengineering (Freeman et al., 2012).

Additionally, alongside the increasing threats to mangrove systems and their microbial processes such as pollution, oil spills, and agricultural run-offs there is current concern regarding the fate of mangroves due to rising sea levels (McKee and Faulkner, 2000; Chambers et al., 2016). An improved understanding of the mechanisms involved in the accumulation of carbon in mangrove ecosystems may provide us with insight into the control of OM accumulation which could help protect mangroves from current and future threats.

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